

DICHOGRAPTID SYNHRABDOSOMES FROM THE ARENIG OF BRITAIN

by J. A. ZALASIEWICZ

ABSTRACT. Dichograptid synrhabdosomes are reported for the first time. Synrhabdosomes of *Didymograptus* aff. *simulans* Elles and Wood from Arenig Fawr, North Wales and *Azygograptus lapworthi* Nicholson from near Keswick, Lake District, are described, both from the Arenig Series (*extensus* Zone). Possible reconstructions of synrhabdosomes of *D.* aff. *simulans* are attempted. It is suggested that synrhabdosomes acted as mechanisms to promote rapid breeding in short-lived, highly favourable environmental conditions.

SYNRHABDOSOMES are comparatively rare associations of graptolite rhabdosomes. Individual rhabdosomes are generally linked at the free distal ends of their virgulae or nemata, although in one recorded instance (Bjerreskov 1976) linkage involves the free ends of proximal virgellae. Biserial (diplograptid) graptolites make up the bulk of known examples (e.g. Ruedemann 1947), but synrhabdosomes have also been recorded amongst uniserial monograptids (e.g. Rickards 1975, p. 414); possible synrhabdosomes of *Dictyonema* (Bulman 1927–1967, p. 27; Ruedemann 1947, pl. 2, fig. 11), and *Corynoides* (Ruedemann 1947, pl. 58, fig. 25) have also been figured. Dichograptid synrhabdosomes have not been described previously. The figured specimens are deposited in the Sedgwick Museum, Cambridge (SM).

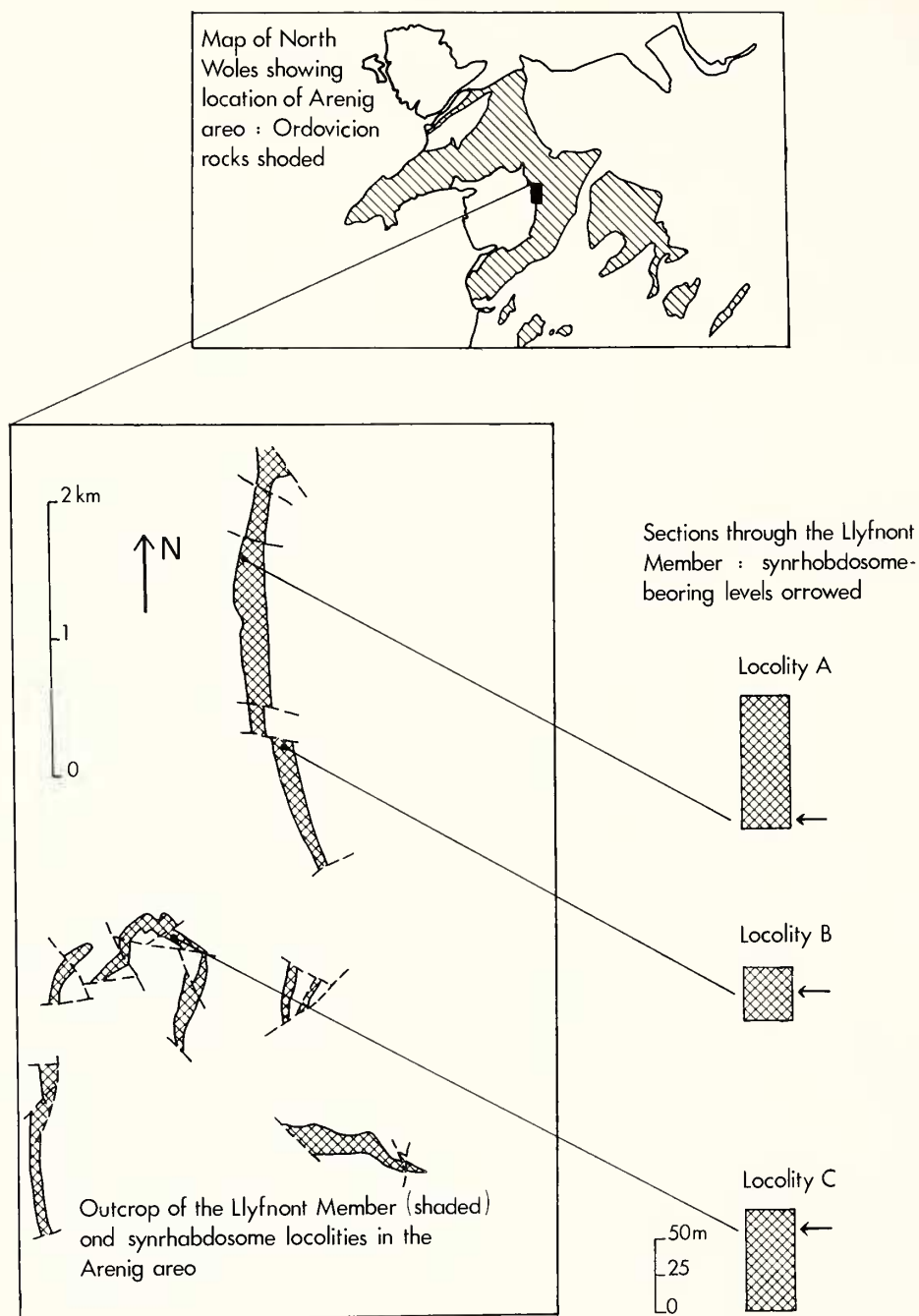
DESCRIPTION OF SYNHRABDOSOMES

Didymograptus aff. *simulans* Elles and Wood, 1901

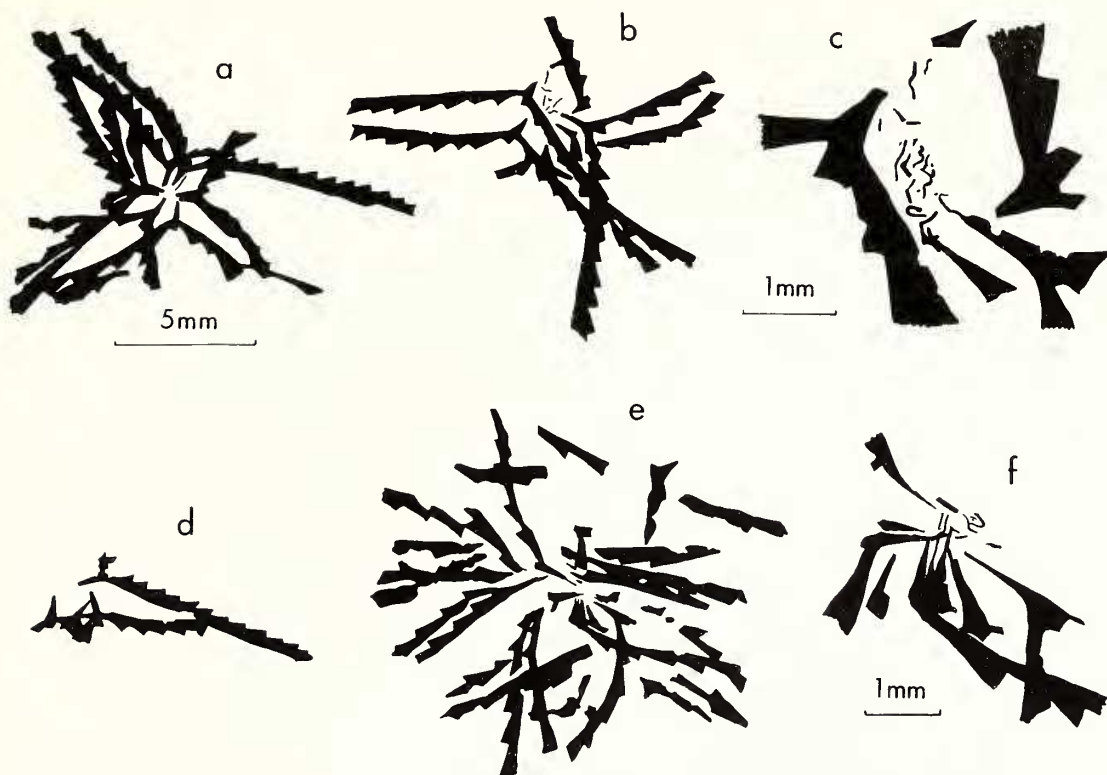
Material. Five synrhabdosomes from three localities in the Llyfnant Member of the Carnedd Iago Formation (lower Arenig Series, *extensus* Zone) of Arenig Fawr, North Wales (text-fig. 1; Zalasiewicz, in press). The Llyfnant Member is dominated by interlayered sandstones and mudstones, containing burrows, loadcasts, and a few ripples (Zalasiewicz 1981). There is little or no grading of individual layers or evidence, such as mudcracks and rainprints, of subaerial exposure. The environment was probably shallow marine subtidal. The only body fossil found *in situ* was *D.* aff. *simulans*, which is locally abundant.

Description. *D.* aff. *simulans* from Arenig Fawr differs from the type material in having a slightly smaller angle between the stipes. The synrhabdosomes are made up of from four to eight rhabdosomes, radially to subradially arranged. The apices of the siculae point towards the centre of the synrhabdosome (text-fig. 2*a, b, d*), and give rise to short, tangled nemata (text-fig. 2*c*). Nemata within synrhabdosomes are locally thickened, up to 0.036 mm across, while nemata of unassociated rhabdosomes do not exceed 0.027 mm across. Preservation of the synrhabdosomes is not good enough to state whether their constituent rhabdosomes are all at the same stage of development.

Discussion. The difference between the nemata of unassociated rhabdosomes and those that form part of a synrhabdosome appears to represent a functional adaptation. However, this does not seem to have been simply a strengthening of the nemata in order to hold the synrhabdosome together, as the thickening is only local (text-fig. 2*c*). In any case, it is likely that synrhabdosomes were held together by soft tissue rather than by the nemata themselves (Rickards 1975, p. 416). Possible reconstructions of synrhabdosomes of *D.* aff. *simulans* are shown in text-fig. 3. The major alternatives are between an ordered (text-fig. 3*a*) and a disordered (text-fig. 3*b*) structure. An ordered structure would have been preferable if most or all *D.* aff. *simulans* rhabdosomes spent most or all of their life-spans as members of synrhabdosomes. However, if synrhabdosomes were temporary structures, or were not formed by all rhabdosomes of *D.* aff. *simulans*, then it may not have been necessary to attain an ordered structure. These general questions are addressed below.



TEXT-FIG. 1. Location and stratigraphic position of synrhobdosomes of *Didymograptus* aff. *simulans* Elles and Wood. Loc. A, spoil from old pits south of Hafotty Ffylltirgerig, NGR SH 8167 3844. Loc. B, 200 m south-east of Beudy Nant-y-pysgod, NGR SH 8202 3703. Loc. C, east face of Moel Llynfiont, NGR SH 8116 3575.



TEXT-FIG. 2. Synrhabdosomes. *a-d*, *Didymograptus* aff. *simulans* Elles and Wood. *a*, SM A102852a–A102860a, loc. B. *b*, SM A102893b–A102898b, loc. A. *c*, proximal part of *b*. *d*, SM A102971–A102975, loc. C. *e*, *Azygograptus lapworthi* Nicholson, SM A17963–A17970, Hodgson Howe Quarry, near Keswick, Cumbria. *f*, proximal part of *e*. *a*, *b*, *d*, *e* to same scale.

Azygograptus lapworthi Nicholson (ex Lapworth MS), 1875

Material. One synrhabdosome in a grey mudstone from the middle Skiddaw Slates (lower Arenig Series, *extensus* Zone) of Hodgson Howe Quarry, near Keswick, Cumbria, England.

Description. At least fifteen rhabdosomes, radially arranged (text-fig. 2*e*). The centre of the synrhabdosome is poorly preserved, but fragments of tangled nemata are visible (text-fig. 2*f*).

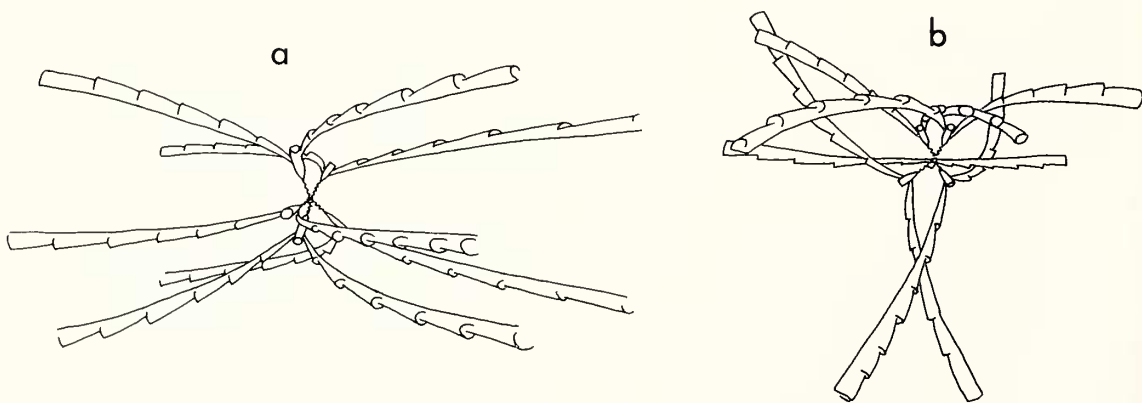
ABUNDANCE, FORM, AND FUNCTION OF SYNHRABDOSOMES

Synrhabdosomes are paradoxical: few species are known to form them, although these species are nevertheless widely scattered both in time and within the graptolite orders. It is commonly implied that this rarity is illusory. Many reconstructions of the Ordovician sea show graptolite synrhabdosomes in the plankton, suspended by their 'floats' (such 'floats' are now known to be artefacts: see Rickards 1975, p. 416). In this view, synrhabdosomes are rare due to post-mortem break-up with, in addition, many synrhabdosomes being overlooked as 'chance associations'. Several features suggest that this view is probably not true. First, where synrhabdosomes have been found they tend to be present in numbers, as in those of *D.* aff. *simulans* described above, and the examples of synrhabdosomes figured by Ruedemann (1947, e.g. pl. 81, fig. 33). Secondly, even moderately well-preserved synrhabdosomes are striking fossils, unlikely to be taken as chance associations. Thirdly,

many species appear to have been physically incapable of forming synrhabdosomes, e.g. *Dicranograptus*, and species of *Dicellograptus* in which the nema is absent or embedded in the dorsal wall of one of the two stipes; in any hypothetical *Cyrtograptus* synrhabdosome the individual graptolites must have been stacked one on top of the other like pancakes—an unlikely structure. Fourthly, any widespread occurrence of graptolites as synrhabdosomes would contradict a most marked evolutionary trend in graptolites, that of the progressive reduction through time in the number of stipes. It follows that synrhabdosomes were relatively rare, yet they possessed advantages that must have overcome the 'disadvantage' of a marked increase in stipe number.

Consider a synrhabdosome-forming species of graptolite. In *Didymograptus* aff. *simulans* it appears that rhabdosomes were not members of synrhabdosomes all of the time, since unassociated rhabdosomes have a straight slender nema, unlike the short, twisted and locally thickened nemata of those within synrhabdosomes. It is also unlikely, for two reasons, that these unassociated rhabdosomes were bound up in synrhabdosomes at some point in their life-cycle. First, the graptolite would have had to discard its nema and grow another to suit its new life-style. Secondly, a numerical argument can be applied: in the case of *A. lapworthi*, several hundred specimens were present on the slabs examined, and only one synrhabdosome was discovered; in the case of *D.* aff. *simulans*, some 120 specimens included five synrhabdosomes. The formation of synrhabdosomes emerges as a strategy indulged in by only some members of a population for what must have been quite particular reasons.

Ruedemann (1895, 1947) described diplograptid synrhabdosomes that included rhabdosomes at all stages of development. In contrast, the rhabdosomes of *Rhaphidograptus toernquisti* joined at their virgellae, that make up the remarkable synrhabdosomes described by Bjerreskov (1976), were all at the same stage of development. Previously suggested modes of development of synrhabdosomes envisage either budding from the apical part of the original sicula (Kozłowski 1949), or the development of a number of siculae from within a mass of extrathecal tissue (Bjerreskov 1976). These imply that the members of any synrhabdosome were either genetically identical, as in the former instance, or were at least kin to each other. Since the most plausible function of the synrhabdosome was to aid sexual reproduction (Rickards 1975, p. 416), both modes of development would have resulted in presumably disadvantageous inbreeding. This disadvantage would have arisen through a reduction in the interchange of genetic material rather than through 'genetic mistakes', a few of which could have been afforded in the likely *r*-selective reproductive regime of the graptolites (D. Grzywacz, pers. comm.). However, if the members of synrhabdosomes were not genetically related, then some



TEXT-FIG. 3. Possible reconstructions of synrhabdosomes of *Didymograptus* aff. *simulans* Elles and Wood. *a*, an ordered structure composed of symmetrically positioned graptolites. *b*, a disordered structure, with randomly positioned graptolites.

clustering together of 'automobile' graptolites must have occurred, perhaps under the influence of some graptolite pheromone. Whether graptolites were capable of 'automobility' (Kirk 1969) remains in doubt (Rickards 1975).

I conclude therefore that the graptolites making up synrhabdosomes were indeed genetically related, that the function of synrhabdosomes was to aid sexual reproduction, and that synrhabdosomes formed only under environmental conditions in which the joint 'disadvantages' of a multi-stipe colony and inbreeding were over-ridden by special circumstances. The special circumstances might have been short-lived, highly favourable conditions, in which synrhabdosomes acted as a mechanism to promote rapid breeding. Given such a function, there would have been little need for synrhabdosomes to obtain the stable ordered structure necessary for an optimum feeding strategy, and those of *D. aff. simulans* would have had the disordered structure shown in text-fig. 3b.

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